Courtship, mating, and cocoon maintenance of Tricca lutetiana (Araneae: Lycosidae)

Petr Dolejš¹, Lenka Kubcová and Jan Buchar: Department of Zoology, Charles University in Prague, Faculty of Science, Viničná 7, CZ – 128 44 Praha 2, Czech Republic. E-mail: dolejs@natur.cuni.cz

Abstract. Tricca lutetiana (Simon 1876) (Lycosidae) lives hidden underground and, thus, is not well known. Our objective was to document more fully basic information on reproduction, particularly copulation, in this species. We obtained and observed in the laboratory 86 individuals from the wild between 2006 and 2008. Vibratory and tactile communication is an important medium during sexual communication. We described unique movements of the mating male's legs during copulation, for the first time in the family Lycosidae. Adult females live for two years and, in their underground burrows, they produce one cocoon per season. They carry the cocoon, mostly using legs IV, and look after it for one month until the offspring leave. Maternal care for spiderlings lasts one week following the spiderlings' emergence.

Keywords: Wolf spider, life history, copulation, tactile communication, Czech Republic

Wolf spiders are famous for their courtship behavior (e.g., Bristowe & Locket 1926; Kaston 1936; Kronestedt 1990; Töpfer-Hofmann et al. 2000; Stratton 2005, and references therein). However, few papers have been published with the sole purpose of describing copulation patterns of certain spider species (e.g., Rovner 1971, 1973; Costa & Sotelo 1994), on cocoon making, and on parental care for cocoons and offspring (e.g., Vlijm 1962; Eason 1964). Montgomery (1903) described life histories of ten lycosid species very precisely, and Engelhardt (1964) described those of four *Trochosa* C.L. Koch 1848 species. Stratton et al. (1996) summarized data on copulation patterns. All those authors focused on common species; however, behavior of rare species has remained unknown.

Tricca lutetiana (Simon 1876) is a European (including Ural), extra-Mediterranean wolf spider (Buchar & Růžička 2002). It ranges from France (Le Peru 2006) in the west to the European central part of Russia (Esjunin et al. 1993) in the east, and from the southernmost part of Scandinavia (Almquist 2005) in the north to Bulgaria (Blagoev 2007) in the south. It has not been found on the British Isles and Pyrenean Peninsula. The species inhabits forest steppes, warm blackthorn shrubs, sun-exposed forest margins, and rock steppes (Buchar & Růžička 2002). Before the use of pitfall trapping in the 1950s, researchers were only familiar with a few specimens from collections (Buchar & Thaler 1995). Therefore, the species was believed to be rare (Wiebes 1956; Braun 1963).

The biology of the species is still almost unknown. Koch (1878) noted that the cocoon of the species is round, white, and reaches five mm in diameter. Wiebes (1956) captured 75 males in May and June using pitfall traps and identified that period as the time of copulation, despite capturing no females. Dolejš (2006) obtained data similar to Wiebes and described the males as nocturnal, active mainly between 03:00–06:00 h under laboratory conditions and compatible with one another in captivity. No exact data on population density are available, but the density seems to be very high on forest/rock steppes, as males of the species are the most abundant

¹Current address: Department of Zoology, National Museum – Natural History Museum, Cirkusová 1740, CZ – 193 00 Praha 9 – Horní Počernice, Czech Republic.

specimens in pitfall traps after a rainy night or in dew (J. Buchar & P. Dolejš pers. obs.).

Wiebes (1956) hypothesized that females may be found conducting yet unobserved sedentary life habits. Dolejš et al. (2008) described burrows of and prey capture by females and juveniles. The burrows are entirely underground, mostly globular and enclosed, with no entrance and no exit leading to the surface. They are situated either under a stone or under the surface without vegetation, reaching at most three cm deep. The burrows are not silk-lined, and spiders prey inside them using the "sit-and-wait strategy." Such a construction of a burrow is unique to this species. Neither juveniles nor females venture out to feed in epigeon (= ground layer; soil surface, spaces under stones, litter, moss and lichen layer, lower herb stems up to five cm). The species hunts small soil animals that enter spiders' burrows when moving through the ground (Dolejš et al. 2008). Probable prey include Enchytraeidae (P. Dolejš pers. obs.), Collembola (Sanders & Platner 2007) and small insect larvae (Doleiš 2006). All these organisms are very abundant in the spiders' locality (P. Doleiš pers. obs.). To date, nobody has studied the phylogeny of this species because it is difficult to find living study animals, as they live hidden in the soil.

Here we followed the appeal by Stratton et al. (1996) to examine more species of lycosids for patterns of copulatory behavior. We focused on *T. lutetiana*, a hidden species that has never been studied before. Our aims were to describe courtship, copulation, and maternal care of the species.

METHODS

We used the methods described in Dolejš et al. (2008) to collect living males, females, and juveniles. The study took place in two National Nature Reserves – NNRs (Dřínová hora in Karlštejn NNR: elev. 345 m, 14°09′39″E, 49°56′30″N, and Koda NNR: elev. 350 m, 14°07′18″E, 49°56′04″N) in Český kras (Bohemian Karst) Protected Landscape Area in the Czech Republic. The Government of the Czech Republic permitted the research in NNRs by the decree no. 1159/07. In this study we used 39 males (eight of them were reared from juveniles) and 47 females (16 of them were reared from juveniles). Voucher specimens (P6A-4926) are deposited in the National Museum (Cirkusová 1740, CZ – 193 00 Praha 9 – Horní Počernice, Czech Republic).

We studied aspects of the biology of T. lutetiana in a laboratory. To imitate adult females' natural conditions and to provide them an opportunity to make burrows, we kept them in glass terraria as described in Dolejš et al. (2008). As the species does not seem to be territorial (we even found three females under one stone in the field), we placed up to two females in one terrarium; nevertheless, we divided the terrarium diagonally in such cases. We held juveniles and males in plastic test tubes (length 10 cm, diameter 15 mm) with wet cotton wool as a source of water. When the juveniles matured into females, we housed them in the terraria as described above. Rearing temperature (day/night: winter = 5/5° C, summer = 26/20° C) followed temperature at the collection sites. We set the photoperiod every week according to the actual sunrise and sunset (winter solstice: 8L:16D, summer solstice: vice versa).

We observed and videotaped (digital Olympus C-7070 WZ camera and Panasonic NV-GS400 video camera) the courtship and mating of focal individuals placed in Petri dishes (diameter 5 cm, depth 14 mm) or directly in the terrarium, where the females lived, at room temperature (21-26° C). To examine substratum and burrow effects on courtship and mating behavior, we conducted the trials in terraria; to describe details that were not observable in terraria, we conducted the trials in Petri dishes. We tested all available adult females with randomly chosen males. Out of 100 trials recorded, we observed and analyzed 37 copulations (29 in Petri dishes and eight in terraria). As our aim was to describe copulation and maternal care, we tested all available females until they mated or produced cocoons. Therefore, we tested nineteen females once and the rest of females multiply. Twelve males (out of 39) copulated once and the rest of males copulated multiply. In total, 32 females (out of 47) mated.

We placed a piece of white, moistened filter paper into the Petri dish to provide a substrate suitable for spiders' locomotion, to improve contrast during videotaping, to allow the spiders to remain hydrated, and to prevent the females from hiding under the paper (females had a tendency to hide under dry filter paper). We placed an adult female into the Petri dish 6-24 h before the trial to allow her to habituate to the new surroundings and deposit silk and pheromones, although moisture in the filter paper could deactivate the pheromones in the female silk (e.g., Vlček 1995). We recorded the spiders' behavior from above for 15 min. That period was all that was necessary. If copulation occurred, it ended before that time was up. For recording in terraria, we chose females whose burrows were situated so that it was possible to effectively record the interactions of both spiders. The period of recording depended on the length of interactions; we videotaped until the copulation ended.

We registered courtship latency, courtship duration, copulation duration and copulatory characteristics (number of insertions, number of side shifts, and behavior of the mating spiders). We designated the moment when a male climbed onto a female as the beginning of copulation, and the moment when the spiders physically separated as the end of copulation.

After copulation, we placed females back in their terraria. Through transparent bottoms of the terraria, we observed the cocoon spinning and maternal care. The cocoons appeared to be adhered to the ventral surface of females' abdomens. In an

attempt to determine the structure responsible, we used a scanning electron microscope JEOL 6380 LV to examine the ventral surface of females' abdomens (n = 4). After the spiderlings left a female, we removed the soil from the terrarium piecewise to count spiderlings.

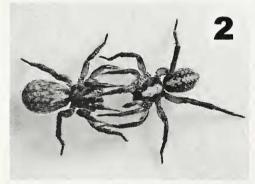
We used the program NCSS 2001 (Number Cruncher Statistical System) (Hintze 2006) to test normality of continuous variables and to calculate descriptive statistics (medians and ranges [R] for data with normal distribution, and medians and quartiles [Q₁, Q₃] for data not normally distributed) on courtship latency, courtship and copulation duration, number of insertions, delay between copulation and making cocoons, lengths of guarding periods and number of offspring. As our data set includes multiple observations and is therefore biased, we used the statistical analysis purely for descriptive use.

RESULTS AND DISCUSSION

Courtship.—In the 29 pairs observed in Petri dishes, all males initiated courtship in 1-2 min (median = 0.84, Q1 = 0.20, $Q_3 = 1.94$, n = 29) after we placed them in the Petri dishes (courtship latency). The males walked in random trajectories and paid attention to holes in the filter paper bitten by females. They were looking for and finally finding the females (n = 23), or were not active and then the females contacted them first (n = 6) using legs I. After locating females, the males usually started to drum with their legs I and II against the substrate and vibrate with their opisthosomas in a vertical plane for 3 s (n = 26). Vibrations of legs and opisthosomas propagate well through soil and thus are useful for burrowing species. Surprisingly, T. lutetiana did not display any behavior commonly known in other wolf spider species: neither palpal drumming nor leg-waving (e.g., Eason 1969). When the males were standing near the female, they jerkily turned towards the females. When standing face to face, the females placed legs I against the males, so females' tarsi I were oriented parallel to the bottom of the Petri dish (Fig. 1). All males contacted females' legs I immediately, using their legs I. After contacting with legs I, they both proceeded to contact with legs II in addition to legs I (Fig. 2) for 2 s. Courtships in Petri dishes lasted nearly 2 min (median = 0.68, $Q_1 = 0.48$, $Q_3 = 1.88$, n = 29) (Fig. 3). Then the males went directly up to the dorsal side of the females. A female signaled her readiness for copulation in a quite unusual way. While, for example, a Trochosa female presses her legs against her body (Engelhardt 1964), a T. lutetiana female never did so, and the females also never produced any vibratory signal. So, her "ready-signal" must be the accurate leg I and II contact with the male, similarly to the "sparring" movements reported in Hogna helluo (Walckenaer 1837) (Kaston 1936; Nappi 1965), or Geolycosa turricola (Treat 1880) (Miller & Miller 1987). However, all three species differ in duration of those movements and in the further behavior of the pair. The reason for that behavior is that a female is sitting in a dark burrow, and thus a male cannot see her position. Bristowe & Locket (1926) also recorded leg contact in pairs of burrowing wolf spiders.

In terraria, the spiders lived in more natural conditions, and we did not measure the courtship latency as the males sometimes hid in a crevice in the ground and did not move





Figures 1–2.—*Tricca lutetiana*, courtship. 1. Female (down) is shifting legs I against a courting male; 2. Both spiders (male on the right) are touching each other using leg pairs I and II.

for a long time (n = 3 out of 8 males). All males courted intensively; they vibrated with all legs. The females' responses were the same as in Petri dishes; all females lifted their legs, thereby breaking the roof of their burrows and making an entrance for the males. However, how males find the entirely closed underground burrows of females and how they know where to court is still unclear. The males could not detect any females' cues deposited on silk, as no threads appeared on the surface above the burrow. Maybe the males could detect some chemical cues deposited by the females on the ground in the burrow. Because the females are present in the burrows all the time and are probably producing chemical cues continuously, it does not matter that the moisture present in the soil could deactivate those cues. Another possibility is communication via airborne olfaction, as in Pardosa milvina (Hentz 1844) (Searcy et al. 1999) and two burrowing Allocosa Banks 1900 species (Aisenberg et al. 2010). Contrary to the situation in the Petri dishes, the males in terraria first retreated and then repeatedly continued courtship, drawing close to the female's now open burrow. Therefore, courtships in the terraria lasted notably longer (median = 8.59 min, R = 1.10-24.17, n = 8)

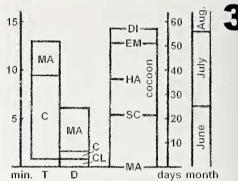


Figure 3.—Tricca lutetiana, typical sequence and the median time spent at each stage of reproduction. C = courtship, CL = courtship latency, D = trial in a Petri dish, DI = dispersion of spiderlings, EM = emergence from the cocoon, HA = hatching in the cocoon, MA = mating. SC = spinning the cocoon, T = trial in a terrarium.

(Fig. 3). Finally, all males mounted the females inside the burrow, and the females did not leave the burrow. Consequently, touching, vibrations, and probably chemical cues are the only possible means of communication between males and females of this species, and thus its courtship contains limited visual signaling. It appears that *T. lutetiana* has complex tactile communication during courtship.

Mating.—The males grasped the females' leg pairs I and II using their leg pairs III and IV, so the females stood on their leg pair III and IV. The latter leg pair was spread broadly (Fig. 4). The in-copula position was as in other lycosid species (e.g., Foelix 1996; Stratton et al. 1996); the males waggled their opisthosomas up and down during copulation, similarly to other wolf spiders (e.g., Kaston 1936). However, the act of copulation of T. lutetiana was surprisingly dynamic. It was unique to the species that all males showed special movements of their legs. When the males copulated with their left pedipalps (Fig. 4), they stroked the females' opisthosoma in the area of the spinnerets (or on its ventral part) using their left leg I. Simultaneously, a male stroked the female's left leg III using his right leg II (Fig. 4). Several males also moved with their left legs II (n = 13). When copulating with the right pedipalp, the male performed the same movements viceversa (for a short video clip see http://web.natur.cuni.cz/ zoologie/invertebrata). Sometimes, the male started those specific movements during the second (n = 8), third (n = 6), or even fourth (n = 4) insertion. Four females contacted the appropriate males' legs if males did not perform those movements.

In terraria, copulation of *T. lutetiana* always occurred inside the females' burrows (i.e., under the surface). Copulations of burrowing wolf spiders studied up to now almost always proceed at the burrow entrance (e.g., Miller & Miller 1987; Stratton et al. 1996), at the level of the surface. Only a few lycosids copulate inside their burrows: *Allocosa alticeps* (Mello-Leitão 1944) (Aisenberg & Costa 2008), *Allocosa brasiliensis* (Petrunkevitch 1910) (Aisenberg et al. 2007),

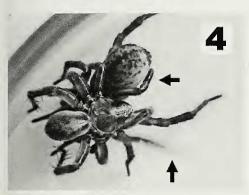


Figure 4.—Tricca lutetiana, mating. Insertion of the left pedipalp, male is moving his left I and right II legs (arrows) and opisthosoma.

Allocosa fasciiventris (Dufour 1835) (Fernández-Montraveta & Ortega 1990), and Xerolycosa mongolica (Schenkel 1963) (Y.M. Marusik pers. comm.). Copulation inside a burrow perhaps leads to the most important feature of T. lutetiana: the peculiar movements in the in-copula position that have not yet been observed in any other wolf spider species. The movements may inform a female that a male is not prey and sexually stimulate her. The former function is supported by the fact that T. lutetiana prevs in the dark inside the burrow (Dolejš et al. 2008), whereas other burrowing wolf spiders venture out for prey (Nyffeler 2000). The copulation is relatively short, so males probably do not have enough time to produce chemical cues (if the males use any). The latter is why some females "encouraged" the males to initiate movements. The movements seem to be a very important feature, and their hypothetical presence in another lycosid species may solve the unclear taxonomical position of T. lutetiana.

When shifting from one pedipalp to the other, the males tapped on the females' opisthosomas. The shifts lasted three to four seconds. We observed six insertions (R = 2-11, n = 31) during copulation. Any subsequent insertion usually lasted longer than the preceding one. Increasing lengths of insertions seem to be a common feature in lycosid copulation, since Montgomery (1903) also observed it. We recorded a male spine erection at the beginning of each palpal insertion (due to increased body pressure during insertion and expansion of the hematodocha [Foelix 1996]). Judging from the male spine erections, there was only a single expansion of the hematodocha per insertion and a single insertion on a side before switching sides. The copulatory pattern of T. lutetiana followed those of eleven wolf spiders listed by Stratton et al. (1996). We recorded that not only the males, but also the females, erected their spines (n = 19) during shifting the pedipalp. This movement (together with swiveling females' abdomens so as to bring the epigynum within reach of the male pedipalp, as it was recorded in other lycosids [Bristowe & Locket 1926; Rovner 1971]) revealed that they were not cataleptic, unlike females of e.g., Trochosa (Engelhardt 1964) or Rabidosa santrita (Chamberlin & Ivie 1942) (Brown 2006). Therefore, it is remarkable that neither males nor females were aggressive toward each other during their cohabitation in the Petri dish (with exception of two females who ate the male before he could begin courtship). No female attacked the male after copulation. That confirms the peaceable behavior of the species observed by Dolejš (2006). If any catalepsy was present in this species, the unique males' leg movement would be of no use.

The copulation in Petri dishes lasted a few minutes (median = 4.35, R = 1.08-9.58, n = 29), similar to a burrowing Arctosa perita (Latreille 1799) (Bristowe & Locket 1926). A short copulation is typical for obligate burrowing species and is related to the more primitive copulation pattern, with one insertion on one side (Stratton et al. 1996). Three males cleaned their pedipalps with their chelicerae following copulation. Surprisingly, no males cleaned their pedipalps during copulation, even though Montgomery (1903) and Lopez (1987) considered it a frequent behavior. We never observed the details of the male's sperm induction. After copulation in the terraria, of similar duration to copulations in Petri dishes (median = 2.15, $Q_1 = 1.79$, $Q_3 = 6.72$, n = 8), the males left the burrow very quickly. In two cases only, the female also left it (see http://web.natur.cuni.cz/zoologie/ invertebrata), but no female attacked a male. Then the females began to repair the broken "roof" of their burrows. They brought small pieces of soil from the bottom of the burrow and stuck them into the open entrance that resulted after the copulation, and secured them with a few isolated threads (n =8) (see http://web.natur.cuni.cz/zoologie/invertebrata). The females' subterranean lifestyle in enclosed burrows places great restrictions on the reproductive behaviors of both males and females, and may be the underlying cause of the differences between T. lutetiana and previously studied lycosids.

Maternal behavior.—Twenty-eight females laid eggs in captivity. Fifteen of them were laboratory mated (86.7% cocoons viable) and thirteen females refused males in the laboratory, so we presume that they had already mated in the field (92.3% cocoons viable). We found that adult females live for two years. The following year (after hibernation), twelve females laid eggs again. Nine of them laid without mating (66.7% cocoons viable) and three females mated in the second year (1 viable cocoon). Thus females are able to store sperm in their receptacula for one year after copulation and need not mate again in the second year of adulthood. All of the females produced only one brood per season (n = 32) at the end of June, three weeks (median = 21 days, R = 3-48, n = 18) after copulation (Fig. 3). Therefore, T. lutetiana differs from many other wolf spider species, whose adult females live for one year and produce two cocoons; e.g., Arctosa cinerea (Fabricius 1777) (Framenau et al. 1996). Only Fernández-Montraveta & Ortega (1990) found similarly long-lived females, also producing cocoons in two years, in Allocosa fasciiventris.

Females always made cocoons in their underground burrows. The cocoons were globular, white, and 3-4.5 mm diam. (year 1, n = 28; year 2, n = 12), as reported Koch (1878). We observed three females during cocoon spinning. Their behavior (see http://web.natur.cuni.cz/zoologie/invertebrata) was similar to that reported by Montgomery (1903), Vlijm (1962), Eason (1964), Engelhardt (1964), and

Table 1.—Cocoon building. Summary of the phases (sensu Montgomery 1903 and Engelhardt 1964) observed in wolf spiders. Time in minutes. SC = spinning a scaffold, BA = spinning a base of the cocoon, MW = spinning a marginal wall on the base, OV = oviposition, CO = spinning a cover of the cocoon, LO = loosening the cocoon from the scaffold, SU = spinning upon the cocoon. * = observed, but without time indication; X = not observed.

Species	SC	BA	MW	OV	CO	LO	SU	Source
Pardosa amentata (Clerck 1757)	*	18	5	*	13	3	*	Vlijm 1962
Pardosa lapidicina Emerton 1885	*	30	*	4-6	25-30	8	16-20	Eason 1969
Pardosa milvina (Hentz 1844)	30	34	5 or X	2-4	12-14	3-4	9-40	Montgomery 1903
Rabidosa punctulata (Hentz 1844)	*	33	13	4–6	20-30	12-25	25	Montgomery 1903; Eason 1964; Eason & Whitcomb 1965
Schizocosa avida (Walckenaer 1837)	*	42	17	3	15	2-5	27	Montgomery 1903
Schizocosa bilineata (Emerton 1885)	*	20	37	5	25	4	24	Montgomery 1903
Schizocosa crassipes (Walckenaer 1837)	* or X	45	14-20	4-5	18-35	2-5	22-25	Montgomery 1903
Tricca lutetiana (Simon 1876)	16	44	X	8	24	4	24	this work
Trochosa spp.	38	65	28	14	27	3	16	Engelhardt 1964

Eason & Whitcomb (1965) (Table 1). The diameter of the cocoon base of T. lutetiana was 7 mm, with a denser middle part (diam. 3.5-4 mm) (n = 3), but without the marginal wall, contrary to the description of the above-mentioned authors.

All the females kept their cocoons in their burrows, and they did not leave the burrows in any situation. In about one-third of the observations, females kept the cocoons fastened to their spinnerets, and the cocoons then swung under the opisthosoma. In the remaining observations, females kept their cocoons under the ventral side of their opisthosoma and held them by leg pair IV under the opisthosoma (Fig. 5). That method of cocoon maintenance seems to be a common feature among lycosids, as we observed it in Alopecosa sulzeri (Pavesi 1873) (P. Dolejš, pers. obs.), and Montgomery (1903) observed it in Hogna helluo. However, while T. lutetiana females were moving, the cocoons were in a stable position. We recorded setae (Fig. 6) with hooked endings (Fig. 7) on the ventral part of the females' opisthosomas (n = 4). Their function is probably to fasten the cocoon to the opisthosoma. Rovner et al. (1973) discussed the function of the hairs in Rabidosa punctulata (Hentz 1844); however, they described the ending of the hairs as "knobbed tips." The explanation of the contrast is in the different magnification used. We examined the hairs of T. lutetiana under magnification 4500-12000×, whereas Rovner et al. (1973) studied those of R. punctulata with magnification $1000-3000\times$.

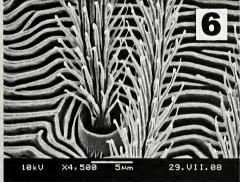
Spiderling emergence.—The juveniles hatched from eggs in the cocoon after 2 wk (median = 15 days, R = 12-19, n = 29), in mid-July (Fig. 3). Hatching was obvious from the increase in diameter of the cocoon, which grew to about 1-1.5 mm. We did not investigate the embryonic and postembryonic stadia in the cocoons. The juveniles left the cocoon through a cleft in the seam after a month (median = 31 days, R = 24-36, n =28), since the females spun the cocoons (in accordance with Eason [1964]) at the end of July (Fig. 3). The juveniles then climbed onto the females' opisthosomas, where they occupied the whole opisthosomal surface; they did not occupy her carapace, unlike some other wolf spiders (e.g., Montgomery 1903; Eason 1964; Engelhardt 1964; Rovner et al. 1973). Females stayed with them in the burrows for nearly one week (median = Q_1 = Q_3 = 6 days, n = 28) (Fig. 3), similarly to most wolf spiders (e.g., Nielsen 1932; Eason 1964; Engelhardt 1964; Foelix 1996).

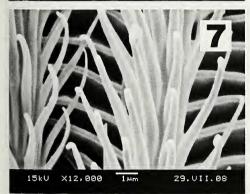
The females with cocoons or spiderlings attached to their bodies caught prey in their burrows (n = 32). That disagrees with the statement of Nyffeler (2000), who concludes that guarding females of burrowing species do not feed, whereas those of free-moving species do. Most burrowing spiders only prey outside the burrows (Nyffeler 2000), whereas T. lutetiana uses its burrows for hunting (Dolejš et al. 2008). On the one hand, females of T. lutetiana carrying cocoons or juveniles have a supply of food without having to leave the burrows. On the other hand, the supply of food under the ground is not probably very rich, and so the females have to take every opportunity to feed.

The females with spiderlings on their opisthosomas left their enclosed burrows in the evening and at night (n = 28) at the beginning of August (Fig. 3). While spherical openings were visible on the soil surface, the burrows remained undisturbed and their walls did not collapse. That suggests that the females were leaving their burrows very gently; otherwise they would damage the walls, since the walls did not benefit from the support of a silk lining. The females then stayed on the surface near their former burrows for one day until all the juveniles left their opisthosomas (n = 22). All the juveniles left the females on the same day. The last juveniles that remained on the females' opisthosomas did not occupy the ventral part of the opisthosomas anymore. After leaving the females, the juveniles searched for cracks in the ground to hide. When the last spiderlings left, the females hid under a stone or underground and made a new, shallow, bowl-like or spherical burrow reaching a depth of 1 to 1.5 cm. Females reared twodozen (median = 24, R = 7-46, n = 32) spiderlings. That is a relatively small clutch size, among burrowing wolf spiders comparable to only a few burrowing lycosids; e.g., Geolycosa xera archboldi McCrone 1963 (Marshall 1995).

Four females behaved quite strangely. They did not leave the burrows, and their spiderlings spread out underground from the mothers' burrows. That was obvious because the spiderlings disappeared from the burrow while the females remained inside the burrows. We saw neither females nor spiderlings on the surface, and we found the spiderlings underground close to their mothers' burrows. Normally when a female left the burrow, we could find the spiderlings underground in all parts of the terratium. This observation documented that an alternative means of dispersing exists.







Figures 5-7.—*Tricca lutetiana*, cocoon keeping. 5. Female is carrying a cocoon under her opisthosoma using legs IV; 6. Pinnate setae on the ventral part of female's opisthosoma; 7. detail of the setae with hooked endings.

Conclusion.—The subterrestrial life of *Tricca lutetiana* influences all its reproductive behavior. As mating occurs underground, the spiders communicate via vibrations and contacts, even during copulation. The sit-and-wait feeding strategy inside the burrow places restrictions on reproduction of this species. Probably because of the low food supply underground, females produce only one cocoon per year. For the same reason, females catch prey in the burrow even when carrying spiderlings.

ACKNOWLEDGMENTS

We would like to thank Jan Mourek and Miroslav Hyliš for help with the scanning electron microscopy. We are indebted to Eva Havliková and Jana Trojanová for correcting our English. We wish to thank Tereza Kořínková for reading our manuscript and giving critical comments. We are very grateful to two anonymous reviewers for valuable suggestions to improve this paper and to the editors of the Journal of Arachnology (Linden E. Higgins and Julie Whitman-Zai) for extensive comments and help. We are indebted to Vlastimil Růžička for sending us important literature and Dagmar Dolejšová for translating the Dutch article. We also thank Yuri M. Marusik for providing us with his unpublished data. This research was fully funded by the Grant Agency of the Charles University: GA UK 208/2005B-BIO/Prf and GA UK 140907.

LITERATURE CITED

Aisenberg, A., L. Baruffaldi & M. González. 2010. Behavioural evidence of male volatile pheromones in the sex-role reversed wolf spiders Allocosa brasiliensis and Allocosa alticeps. Naturwissenschaften 97:63–70.

Aisenberg, A. & F.G. Costa. 2008. Reproductive isolation and sex role reversal in two sympatric sand-dwelling wolf spiders of the genus *Allocosa*. Canadian Journal of Zoology 86:648–658.

Aisenberg, A., C. Viera & F.G. Costa. 2007. Daring females, devoted males, and reversed sexual size dimorphism in the sand-dwelling spider Allocosa brasiliensis (Araneae, Lycosidae). Behavioral Ecology and Sociobiology 62:29–35.

Almquist, S. 2005. Swedish Araneae, Part 1. Families Atypidae to Hahniidae (Linyphiidae excluded). Insect Systematics & Evolution Supplement 62:1–284.

Blagoev, G. 2007. Fauna and zoogeography of wolf spiders (Araneae: Lycosidae) in Bulgaria. Pp. 469–480. In Biogeography and Ecology of Bulgaria. (V. Fet & A. Popov, eds.). Springer, Dordrecht, Netherlands.

Braun, R. 1963. Das *Tricca*-Problem (Arach., Araneae). Senckenbergiana Biologica 44:73–82.

Bristowe, W.S. & G.H. Locket. 1926. The courtship of British lycosid spiders, and its probable significance. Proceedings of the Zoological Society of London 22:317–347.

Brown, C.A. 2006. Observations on courtship and copulation of the wolf spider *Rabidosa santrita* (Araneae, Lycosidae). Journal of Arachnology 34:476–479.

Buchar, J. & V. Růžička. 2002. Catalogue of Spiders of the Czech Republic. Peres. Praha.

Buchar, J. & K. Thaler. 1995. Die Wolfspinnen von Österreich 2: Gattungen Arctosa, Tricca, Trochosa (Arachnida, Araneida: Lycosidae) – Faunistisch-tiergeographische Übersicht. Carinthia II 185/105/481–498.

Chamberlin, R.V. & W. Ivie. 1942. A hundred new species of American spiders. Bulletin of the University of Utah 32(13):1–117. Costa, F.G. & J.R. Sotelo. 1994. Stereotypy and versatility of the copulatory pattern of *Lycosa malitiosa* (Araneae, Lycosidae) at cool versus warm temperatures. Journal of Arachnology 22:200-204.

Dolejš, P. 2006. Životní cyklus a eko - etologické projevy slíďáka Tricca lutetiana (Araneae: Lycosidae) (Study of the life cycle, ecology and ethological behaviour of Tricca lutetiana [Araneae: Lycosidae]). B.Sc. thesis, Charles University in Prague, Praha (in Czech, English abstract).

Dolejš, P., L. Kubcová & J. Buchar, 2008, Subterrestrial life of Arctosa lutetiana (Araneae, Lycosidae). Journal of Arachnology

36:202-203.

Eason, R.R. 1964. Maternal care as exhibited by wolf spiders (lycosids). Arkansas Academy of Science Proceedings 18:13-19.

Eason, R.R. 1969. Life history and behavior of Pardosa lapidicina Emerton (Araneae: Lycosidae). Journal of the Kansas Entomological Society 42:339-360.

Eason, R. & W.H. Whitcomb, 1965. Life history of the dotted wolf. spider, Lycosa punctulata Hentz (Araneida: Lycosidae). Arkansas

Academy of Science Proceedings 19:11-20.

Engelhardt, W. 1964. Die mitteleuropäischen Arten der Gattung Trochosa C. L. Koch, 1848 (Araneae, Lycosidae). Morphologie, Chemotaxonomie, Biologie, Autökologie, Zeitschrift für Morphologie und Ökologie der Tiere 54:219-392.

Esjunin, S.L., S.I. Golovatch & L.D. Penev. 1993. The fauna and zoogeography of spiders inhabiting oak forests of the East European Plain, Berichte des Naturwissenschaftlich-Medizinischen

Vereins in Innsbruck 80:175-249.

Fernández-Montraveta, C. & J. Ortega. 1990. Some aspects of the reproductive behavior of Lycosa tarentula fasciiventris (Araneae, Lycosidae). Journal of Arachnology 18:257-262.

Foelix, R.F. 1996. Biology of Spiders. Second edition. Oxford

University Press, New York.

Framenau, V., M. Dieterich, M. Reich & H. Plachter, 1996. Life cycle, habitat selection and home ranges of Arctosa cinerea (Fabricius, 1777) (Araneae: Lycosidae) in a braided section of the Upper Isar (Germany, Bavaria). Revue Suisse de Zoologie Supplement 1:223-234.

Hintze, J. 2006. NCSS, PASS, and GESS. NCSS. Kaysville, Utah. Online at http://www.ncss.com.

Kaston, B.J. 1936. The senses involved in the courtship of some vagabond spiders. Entomologica Americana 16:97-167.

Koch, L. 1878, Verzeichniss der bei Nürnberg bis jetzt beobachteten Arachniden (mit Ausschluss der Ixodiden und Acariden) und Beschreibungen von neuen, hier vorkommenden Arten. Abhandlungen naturhistorisch Gesellschaft Nürnberg 6:113-198.

Kronestedt, T. 1990. Separation of two species standing as Alopecosa aculeata (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the pulverulenta group (Araneae, Lycosidae). Zoologica Scripta 19:203-225.

Le Peru, B. 2007. Catalogue et répartition des araignées de France.

Revue Arachnologique 16:1-468. Lopez, A. 1987. Glandular aspects of sexual biology. Pp. 121–132. In

Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Marshall, S.D. 1995. Natural history, activity patterns, and relocation rates of a burrowing wolf spider Geolycosa xera archboldi

(Araneae, Lycosidae). Journal of Arachnology 23:65-70. McCrone, J.D. 1963. Taxonomic status and evolutionary history of the Geolycosa pikei complex in the southeastern United States (Araneae, Lycosidae). American Midland Naturalist 70:47-73.

Mello-Leitão, C.F. de. 1944. Aranas de la provincia de Buenos Aires. Revista del Museo de La Plata (N.S., Zoología) 3:311-393.

Miller, G.L. & P.R. Miller. 1987. Life cycle and courtship behavior of the burrowing wolf spider Geolycosa turricola (Treat) (Araneae.

Lycosidae). Journal of Arachnology 15:385-394.

Montgomery, T.H. 1903. Studies on the habits of spiders, particularly those of the mating period. Proceedings of the Academy of Natural Sciences of Philadelphia 55:59-149.

Nappi, A.J. 1965. Notes on the courtship and mating habits of the wolf spider Lycosa helluo Walckenaer. American Midland Natu-

ralist 74:368-373.

Nielsen, E. 1932. The Biology of Spiders, with Especial Reference to the Danish Fauna. Volume I. Levin & Munksgaard, Copenhagen. Nyffeler, M. 2000. Do adult female lycosids feed during the period of

maternal care? Bulletin of the British Arachnological Society 11:388-390.

Rovner, J.S. 1971. Mechanisms controlling copulatory behavior in wolf spiders (Araneae: Lycosidae). Psyche 78:150-165.

Rovner, J.S. 1973. Copulatory pattern supports generic placement of Schizocosa avida (Walckenaer) (Araneae: Lycosidae). Psyche 80:245-248.

Rovner, J.S., G.A. Higashi & R.F. Foelix. 1973. Maternal behavior in wolf spiders: The role of abdominal hairs. Science 182:1153-1155.

Sanders, D. & C. Platner. 2007. Intraguild interactions between spiders and ants and top-down control in a grassland food web. Oecologia 150:611-624.

Schenkel, E. 1963. Ostasiatische Spinnen aus dem Muséum d'Histoire naturelle de Paris. Mémoires du Muséum national d'Histoire naturelle de Paris (A, Zoologie) 25:1-481.

Searcy, L.E., A.L. Rypstra & M.H. Persons. 1999. Airborne chemical communication in the wolf spider Pardosa milvina. Journal of Chemical Ecology 25:2527-2533.

Stratton, G.E. 2005. Evolution of ornamentation and courtship behavior in Schizocosa: insights from a phylogeny based on morphology (Araneae, Lycosidae). Journal of Arachnology 33:347-376.

Stratton, G.E., E.A. Hebets, P.R. Miller & G.L. Miller, 1996. Pattern and duration of copulation in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 24:186-200.

Töpfer-Hoffman, G., D. Cordes & O. von Helversen, 2000, Cryptic species in the Pardosa lugubris group (Araneae, Lycosidae), with description of two new species. Bulletin of the British Arachnological Society 11:257-274.

Vlček, K. 1995. The wolf spider Pardosa alacris (Araneae, Lycosidae): the courtship display of this and related species and pheromone communication. Pp. 174-183. In Proceedings of the 15th European Colloquium of Arachnology, České Budějovice 1995. (V. Růžička, ed.). Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic.

Vlijm, L. 1962. Vorming van de eicocon bij de Wolfspin Pardosa amentata (Lycosidae). De Levende Natuur 65:25-28.

Wiebes, J.T. 1956. Tricca lutetiana Simon, a rare spider, new to the Dutch fauna (Araneae, Lycosidae). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (C) 59:405-415.

Manuscript received 6 April 2009, revised 3 August 2010.